

specimens of it were sent to Dr. Grenier, and that he called it the *E. tetragonum* of the 'Flore de France.' In that determination he was assuredly in error, for the plant can belong to no other species described in that admirable work than *E. palustre* or *E. virgatum* (the *E. obscurum* of this paper). In obtaining and quoting the opinion of either of the authors of that 'Flora,' it should be remembered that, although the work is a joint production, each portion has its own individual and declared author. Dr. Godron is the author of the account of the genus *Epilobium*. In such cases as this, Dr. Grenier may know no more than the inquirer about the subject upon which he is consulted.

[To be continued.]

XX.—*On the Mechanism of Aquatic Respiration and on the Structure of the Organs of Breathing in Invertebrate Animals.*
By THOMAS WILLIAMS, M.D. Lond., F.L.S., Physician to the Swansea Infirmary.

[Continued from p. 154.]

The Glands contained in the Respiratory Cavity of Branchiferous and Pulmoniferous Gasteropods.

THE respiratory cavity of all Cephaloporous Mollusks, in addition to the organs of breathing, lodges one, two or more glandular bodies, the structure and office of which are the subject even at the present time of dispute among comparative anatomists. In different genera these glands affect different relative positions in the cavity.

In some instances they are near and parallel to the rectum, in others they encircle the heart, in others they constitute a mass lying only on one side of this organ. Many of the Pectinibranchs are provided with two glands, in the space between which on the roof the branchia is situated.

By Cuvier they were called the muciparous glands. Dr. Sharpey has supposed the one to be a supplementary branchia, the other he has designated after Cuvier the mucous gland. By Swammerdam, Poli, Blumenbach and the elder anatomists, they were supposed to be concerned in the secretion of calcareous salts. Bojanus conceived that the glands contained in the breathing-chamber of the higher Gasteropods were homologous with certain glandular bodies described by him in the Lamellibranchs, in both holding a similar relation to the branchiæ. As he had proved the latter to be kidneys, he inferred that the former must be so also. The alleged muciparous glands of the

Gasteropods were believed by Meckel* to constitute the true renal system of these animals. A new demonstration of their renal character was subsequently rendered by Jacobson† by the discovery of uric acid in the substance of these glands. His researches comprised analyses of the glands of *Helix pomatia*, *Limax niger*, *Lymneus stagnalis* and *Planorbis cornea*. Jacobson's views, however, had been anticipated by Döllinger and Holmlich‡, who had long previously indicated these glands as the real kidneys of these animals. It is stated by Siebold and Stannius§ that in the dried kidneys of *Helix pomatia* and *Paludina vivipara*, when treated with nitric acid and ammonia, considerable quantities of murexid may be discovered. Treviranus has descended to the minuteness of asserting that in these Gasteropods a portion of the pulmonary or branchial, recently arterialized blood passes through the kidneys in its path to the auricle. In another place in their excellent work, Siebold and Stannius observe that in the Pectinibranchs the kidney is replaced by a gland which is situated behind the branchia between the heart and the liver, and which in the marine species secretes the purple liquid. This is the gland which Dr. Sharpey has described as a bipectinate and supplementary gill.

Kidneys have also been described by Quoy and Gaimard, under the several names of muciparous glands, organ of the purple, depurating organs, &c., in *Phasianella*, *Turbo*, *Buccinum*, *Mitra*, *Oliva*, *Caprea*, *Harpa*, *Dolium*, *Cassis*, *Purpura*, *Fusus*, *Auricula*||. Leydig has also given an account of the renal siphon of *Paludina Vivipara*. More recently Mr. Huxley¶ has expressed his belief in the correctness of the prevailing views as to the true renal nature of the glands contained in the breathing-chamber of the branchiferous and pulmoniferous Gasteropods, and has adopted as conclusive of all doubts, the results obtained by the lithic acid tests in the hands of Jacobson, Meckel and Kölliker**.

The preceding outline of the literature of the question which relates to the renal system of the Invertebrata will suffice to reveal a chaos out of which it does not seem easy to evoke aught that is orderly and consistent. It is evident that the same names have been applied by different observers to very

* Müller, Arch. 1846, p. 13. taf. 1.

† Müller's Arch. vi. 1846.

‡ Dissertatio de Helice pomatia. Hirceb. 1813, p. 23.

§ Comparative Anatomy of the Invertebrata, transl. by Burnett, p. 253, note 3.

|| Voyage de l'Astrolabe, Zoologie, ii.; or Isis, 1834, p. 285; 1836, p. 31.

¶ "On the Morphology of the Cephalous Mollusca," Phil. Trans. 1853.

** Entwicklungsgeschichte der Cephalopoden.

different organs. No clear views as to what should and what should not be characterized as distinctive of a renal organ in the Invertebrate animals, have ever been defined by anatomists. If a marked uniformity of structural type and plan runs through the entire series of other organs in the Invertebrata, such as the biliary, respiratory, circulatory, digestive, &c. systems, the inference is highly probable that a similar serial consistency of plan presides over the renal system. If such be the case in the Vertebrate, why should it not be so in the Invertebrate series? In another place* the author has shown, that the fluids, viewed as chemical and vital solutions, grow more and more simple as the zoological scale is traced downwards (or more and more complex as it is followed upwards); he thence argues that the same tendency to simplification is also manifested by the systems of the solid organs. This is the true science of the comparative anatomy of organs. Their history in this sense has never been written. If the true relation between the solid machinery of the glands and the fluids could be established, it would be most certainly discovered that at the point in the descending series at which a given constituent of the fluids, which a given gland was specially designed to withdraw, ceased to exist, the gland would also cease to exist. The proposition when thus enounced assumes almost a necessary certainty. The mind feels at once assured that no other law can explain the facts, which are indubitable. Anatomists have always worked on the presumption that the fluids of the lowest animal *must* have the same composition as that of the highest, and that consequently the necessities of the organism in the two instances must be the same. If the highest animal be provided with a kidney, therefore the lowest must be endowed with the same organ. Up to this æra in physiology, such in truth has been the fallacious reasoning by which the most distinguished cultivators of this science have conducted their researches. The same observation applies to the secreted products of the physiological actions of organs. It is supposed that because certain ingredients are found to exist under all circumstances in the secretions of the higher animals, consequently the same principles *must* exist in those of the lowest. This false logic has led astray the minds of men for an entire century. There may be nothing in common between the bile of the Mammal and that of the Cephalopod, yet each may be the product of the action of a *liver*. The same reasoning applies to the urinary secretion and to the renal system. Urea and lithic acid, the supposed basis and essence of this secretion

* "On the Chemistry, Physiology and Pathology of the Blood," in the British and Foreign Medico-Chirurgical Review for 1853-4.

in the urine of the Vertebrated animal, are not *necessarily* to be regarded as the basis and essence of the analogous secretion of the lowest Invertebrata. If such reasoning were grounded on truth, it would involve a ridiculous paradox to deny that the minute anatomy of this system of glands was not precisely the same in every grade of the series. But it may be proved immediately, and most readily, that the Malpighian coils of capillaries, so constantly and essentially distinctive of the kidney even of the lowest Vertebrated animal, disappear *in toto* from that of the Gasteropods and the Cephalopod. Here, at the very first step, the fundamental structural element of the higher phase of the organ vanishes. If it be so, is it not reasonable to infer that a correspondingly marked and essential change has occurred in the secreted product of each organ?

The preceding observations, general though they may be, are abundantly sufficient to justify the assertion, that in the present state of knowledge with reference to the comparative histology of the renal system, and the comparative chemistry of the renal secretion, the physiologist is not in a position to state with certainty and confidence whether the alleged kidneys even of the higher cephalous Mollusca are really so or not*.

As the complete history of the glandular bodies which are lodged in the respiratory cavity of the cephalous Mollusca will rightly fall within the compass of another series of researches, the author on this occasion will give only a slight sketch of their structure, and that more because they are constant attendants on the respiratory organs in this class of animals, and occupants of the chamber dedicated to respiration, than because they are asserted by some anatomists to be muciparous glands, and by others no less distinguished as true kidneys.

That gland (Pl. XI. fig. 1 *c'*, *c'*, and fig. 3 *g*) which Cuvier first designated "l'organe de la mucosit ," is unquestionably traceable as one and the same body throughout various changes

* During my recent studies among the Invertebrata, I have accumulated a large mass of materials elucidatory of the serial anatomy of the renal system. It would be quite irrelevant to enter further into details in this place and upon this occasion. I trust that for such a task another opportunity will occur. I am deeply impressed with the belief that real service will be rendered to the comparative anatomy of the Invertebrata even by the publication of such results as have already been attained. It is certain that the urea and uric acid tests, in determining the renal or non-renal character of supposed kidneys in the case of the lower and lowest Invertebrata, lead to conclusions utterly unworthy of confidence. This point I have abundantly proved. The presence of uric acid in the renal secretion supposes a highly nitrogenous or proteinized composition of the blood,—in fact, such complex conditions as do not exist in the fluids of the lower invertebrated animal.

of form and place and size, in all the pectinibranchiate and pulmonated Gasteropods. Under all diversities, it is identifiable by its anatomical structure. Cuvier thus defines its office and locality: "Le rectum, et oviductus de la femelle rampent aussi le long du côté droit de cette cavité, et entre eux et les branchies est un organe particulier composé de cellules recélant une humeur très-visqueuse, servant à former une enveloppe commune, qui renferme les œufs et que l'animal dépose avec eux*." That gland which in *Buccinum* is situated between the rectum on the right and the branchia on the left (when the roof is *in situ*), and attached to the roof of the branchial chamber, is the same gland with that which in *Limax niger* (fig. 1 c, c) lies on the floor of the pulmonary cavity, is extended in figure, and circumscribes a space in the centre of which the heart is situated. These two examples will serve to indicate the extremes of figure and locality which one and the same gland may assume even in kindred genera.

In the Littorinidæ (fig. 7 f) it affects the same position on the roof between the branchia and the rectum.

In the Helicidæ (fig. 3 g) it appears under the form of an oval mass, situated still on the roof of the pulmonary cavity; and, when the parts are *in situ*, to the right of the heart. Thus in the particular of locality, this gland in *Helix* differs remarkably from that of *Limax*, in which it is placed on the floor (fig. 1 c, c) of the cavity. In the Lymneadæ it is observed to occupy the same situation as it does in the Helicidæ. The Planorbidæ are too small to render it practicable to examine this gland separately; but, as in the former family, its position is on the roof and on the right of the heart.

That gland which by Dr. Sharpey has been called the supplementary and doubly laminose gill, is a totally different organ from the former. It does not exist under any form in the pulmoniferous orders. It is largest and most developed in *Buccinum*; in the Periwinkle it is also very distinctly observable. It is situated always to the left of, and parallel to, the branchia. It is invariably tinged with a dark green colour. It terminates anteriorly in a long excretory duct which travels under the membrane of the vault and ends near the rectum.

By Cuvier, and all systematic naturalists, it is believed to be the organ which secretes the "purple and other dyes" which these animals are capable of pouring out, and has been accordingly designated the "colour-gland." In relative position and in general and minute structure, it is readily distinguishable from the "organe de la mucosité" of Cuvier.

* Règne Animal, vol. sur les Mollusques.

The author's purpose at present is simply to present a sketch of the structure of these glands. No opinion with reference to their function can assume a stable and reliable form which is not supported by the results of other researches into the structure of the corresponding organs of other classes of invertebrate animals. This more extended task is reserved for another occasion.

Although in *Limax* the so-called "muciparous gland" differs both in figure and situation from that of *Buccinum*, in minute structure they are not only similar but identical. The folds of which these bodies are composed were called the "*feuillets muqueux*" by Cuvier. They are attached to the internal face of a sort of a *tunica propria*, by which the entire gland is closely bound down. This tunic, regarded in its length, forms a cylinder. The axis of this cylinder is an open space. The sides bear the glandular folds. A transverse as well as a longitudinal section of the gland is required in order to display the true disposition of the glandular laminae.

These bodies are richly ciliated both within and without. Each fold ends in an excretory duct. The ducts emanating from each fold are tributary to a common duct which runs along the axes of the gland and joins the rectum at different points in different genera. This fact, which can be readily verified, is worthy of remembrance. From this fact alone the conclusion is beyond dispute, that if these glands be the real bodies by which the "mucosity" with which, almost at will, the respiratory cavity in these animals may be filled, it can only attain this cavity by oozing through or transuding the *tunica propria* of the gland,—a conclusion repugnant to reason, and at variance with all physiological analogy.

In *Buccinum* the gland is flatter and less cylindrical than in *Limax*. This occasions a slight difference in the mode in which the laminae (fig. 8 *a*) are attached to the *tunica propria*. It is by no means difficult to detach a single fold (*a*) in a perfect state and place it under the microscope. By this simple expedient the entire machinery of this gland is rendered at once evident.

A highly ciliated membrane, more delicate than, although the prolongation inwards of, the *tunica propria*, gives its form to, and contains the gland-substance of, this fold. The external surface of this membrane, although within the boundary of the *tunica propria*, is not the true interior of the gland. The true interior spaces of the gland communicating with the duct are not ciliated; nor is the *internal* surface of the rectum in which it terminates. It will be seen that the entire mass of the glandular fold or lamina under examination consists of two elements: first, the Florence-flask-shaped vesicles (fig. 8 *b*, *b*, and *B*, *b*),

which may not incorrectly be said to represent the lobuli or acini of the glands of the vertebrated animal; and, secondly, the intermediate stromatous and cellular structure which fills up the spaces *external* to and between the vesicles. In the recent gland these two parts are so evidently distinct, and indeed so easily distinguishable, that they cannot be confounded. The cells (B, *b*) *within* the vesicles are densely crowded with semi-fluid albumen-looking contents, of low refractive power. The substance contained in these intravesicular cells is unquestionably *the* secretion of this gland. There it is, directly under the eye, in its very place of production. If by micro-chemical analysis its composition while thus isolated in cells could be determined, the problem as to the real nature and office of this gland might indeed very readily be solved; but the minuteness of the quantity thus presented to the eye renders such a determination impossible.

The nucleated cells (*c*) which occupy the interspaces between the cæcal vesicles are much larger than those contained within these parts; they are densely filled with oleous granules (*d*) of a greenish-yellow colour and of high refractive index. The nucleus in these cells is filled only with an albuminous formless semifluid substance. In this respect they will be found to contrast strikingly with the similarly placed cells of the "colour-gland" afterwards to be described. These extra-follicular cells, so densely charged with a secreted product, perform obviously an important part in the office of these glands. They are separated from those within the vesicles only by the walls of the follicles (B, *e*) themselves. These walls consist literally of only a *hyaline membrane*, structureless, answering simply and exclusively the mechanical purpose of a liminary or circumscriptive sac. No cell-elements are contained in its substance. It is evident therefore that the cells are the real factors in the act of secretion. The large pregnant cells (B, *e*), which stand on the outside of the cæcal follicles of the gland, are *soaked* in the circulating fluid. It surrounds them on all sides. But the blood does not penetrate in mass into the interior of the vesicles. The cells therefore by which these vesicles are filled cannot derive their contents directly from the blood. From the relative position of these parts—the blood, the extra-follicular or stromatous cells, and the intra-follicular cells,—it seems highly probable that the blood is first subjected to the agency of the externally situated cells which cluster around the grape-shaped ends of the glands, and that the prepared contents of these cells pass thence by endosmose into the interior of the follicles, where they for the second time conduce to form, and where they undergo the

elaborative reaction of, a second system of cells. These last cells (B, *f*) are very unlike the former. In the gland of *Helix aspersa* they are best seen. Those which are disposed around the circumference of the space enclosed by the cæcum of the gland are the largest, and each of these cells contains a very apparent nucleus which is charged with greenish-yellow granules. As the eye approaches the centre of the cæcum, the cells lose their nuclei and become filled only with a mucus-like, pellucid, semifluid substance, which eventually escapes into the excretory channels of the gland. In the gland of *Buccinum* the dark nuclei of the circumferential cells (B, *f*) are much less distinct. But the mass of cells by which the cæcum is filled presents the same characters as in *Helix*. It is impossible here to avoid the reflection that the *cells* are considerably larger in size and more numerous in the glands of an Invertebrated than in those of a Vertebrated animal. In that of the latter, a network of blood-vessels accurately fits over and embraces externally the cæcal extremities of the gland. In the Invertebrate animal all glands are constructed in this respect on one general type. The blood courses in large streams through the stromatous substance; it never penetrates the hyaline membrane of the follicle. Those parts of the blood which are appointed to nourish the cells upon the agency of which the act of secretion depends, and which cells in their turn furnish the final secreted product, are destined therefore to pass through an external stratum of cells and through the basement or hyaline membrane of the follicle before they eventually reach the true secreting cells. This exemplifies the important part taken by cells in the act of secretion.

Let the physiologist now review the apparatus whose anatomical constitution has in part been defined. A large excretory duct (fig. 8, B, *g*), discharging its contents into the rectum, is traceable as other ducts into a constantly diminishing series of ducts, until at length the Florence-flask-shaped terminal vesicles (B, *e*) are reached. At this point the microscope discloses a complex system of cells and channels for the transmission of fluid,—a machinery in fact which is little inferior in intricacy to that of the glands of the highest animal. It may be reasonably inferred, that such an organized arrangement in a group of animals comparatively inferior must be designed to furnish a product far more important than the “mucosity” as supposed by Cuvier. It is next to impossible that this secretion can be any other than the *urine*. But this conclusion should receive all the certainty of an unquestionable demonstration, since, in this case, these bodies in the Gasteropods may be recognized

as a starting-point of great value in the determination of analogies and homologies in the lower members of the series. This demonstration is reserved for another opportunity.

A second and much smaller gland exists in the respiratory cavity of the Pectinibranchiata, which hitherto has been variously called the "colour-gland" and the bipectinate supplementary gill. This body is not present in the breathing-chamber of the Pulmonata. In *Helix* a fringe-like fold (fig. 3 *e*) of the membrane of the cavity assumes almost the appearance of a gland; it is however nothing but a portion of the vascular respiratory membrane.

The so-called colour-gland is best studied in *Buccinum* and the Littorinidæ. In both it is situated on the extreme of the roof of the cavity, being separated from the other gland by the interposition of the branchiæ. It is considerably smaller in the Periwinkle than in the Whelk. It has a dark green colour. It commences posteriorly in a cæcal extremity. It is prolonged anteriorly into a tube or duct which travels underneath the mucous membrane of the vault until it approaches the termination of the rectum, where it has its outlet by a separate orifice. Viewed as an axis (fig. 9 *a, a*), this duct may be described as supporting the lobes or leaves (*b, b*) of the gland,—as symmetrical, bilateral, ramose diverticula. This gland presents a general exterior resemblance to the so-called "muciparous gland" of this chamber. It admits of division into two parts—the *lobes* first, which correspond with the laminæ; and, secondly, the *lobuli* (*c*) into which the lobes (*b, b*) are further subdivided. One of the *lobuli* in minute structure represents the arrangement of the whole gland. These *lobuli* do not exist in the "muciparous gland." This is one distinctive fact. The next is that the latter gland has a yellow colour, the former is of a dark green. But distinctions more essential than the preceding remain to be indicated. A lobule is represented by a bunch of grapes flattened (fig. 10). The grapes or terminal follicles (*a, a*) do not exhibit the same *figure* or shape as they do in the "muciparous gland;" they are more elongated and conical. From the latter they differ also in their contents. They circumscribe cells which cannot be confounded with those of the muciparous gland of the respiratory cavity. The stromatous tissue (fig. 10 *b*) which envelopes the *cæca* is obviously dissimilar from that of the latter gland. The dark green colour (*c*) of both the extracæcal and intracæcal cells is one striking fact of distinction. This colour is seated in the *nuclei* of the cells. Like those of the "muciparous gland," these cell-elements are divisible into two groups; those, first, which are external to the cæcum; and, secondly, those which are within (*d*). Those which are with-

out are of a deep dark green colour (*c*); this colour is concentrated in the nucleus. Those which are within the limitary membrane of the cæcum are less darkly tinged (*d*). But it is evident that the latter cells circumscribe contents which are the derivative products of the former. The cells situated in the circumference of the vesicles are more dark than those placed in the centre. This gradation of colouring is expressive of the stages through which the secreted product passes. By this coloured substance this gland is strikingly distinguished from that of the "muciparous gland." The follicles differ in figure from those of the latter, but the cells do not; they are distinguished only by the colour of the material by which they are filled.

Arbitrating as mere physiologists, it would be quite impossible to say why one of these glands should be a kidney and why the other should not. It cannot be proved by the secreted product of this gland that it is one really designed to furnish a "coloured fluid." This inference is founded simply upon the colour of the cell-machinery by which this product is elaborated—not upon the colour of the finished excretion.

The author proposes for the present to leave this question in an unsettled attitude; but he will venture to state that neither of these glands is the source of the "mucus" or "mucosity" for which the Gasteropod Mollusks are remarkable. This "mucosity" is really supplied by a totally different machinery. It is poured forth by follicles which in all Gasteropod and Nudibranchiate Mollusks are more or less thickly strewn over the mucous and cutaneous surfaces. These follicles will be more minutely described in speaking of the respiratory organs of the Nudibranchiate Mollusks.

EXPLANATION OF PLATES V. AND XI.

PLATE V.

- Fig. 1.* Animal of *Littorina littorea*, removed from its shell, having the branchial chamber laid open,—the roof being everted in order to show its under or internal surface. *e, e*, roof; *d*, colour-gland of the author, "double"-gill of Dr. Sharpey and other naturalists; *a, a*, branchia, consisting of many hundreds of parallel leaves; *b*, a gland of the mucosity, supposed to have a renal function; *c*, extremity of the *intestinum rectum*; *g*, a second gland whose function is not determined; *j*, duct of the generative organ; *i*, floor of the branchial chamber; *h*, mantle; *k*, abdominal portion of the body.
- Fig. 2.* Animal of *Buccinum undatum*, removed from its shell, and showing the roof of the respiratory chamber everted: *f*, siphon; *b*, the so-called double-gill, the colour-gland of the author; *a, a'*, branchia, consisting of many hundreds of parallel leaves; *d*, duct leading from the colour-gland and terminating near the rectum, *e*; *c*, gland of the mucosity, supposed to have a renal function.



